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Selection of Genotypes Tolerant of Aluminium and Manganese

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I. INTRODUCTION

Species vary in their reaction to soil acidity. However, the last 25 years has seen the recognition that differences also exist among genotypes within a species (Ouellette and Dessureaux, 1958; Neenan, 1960). Differential tolerances to aluminium within species have been reported for barley, wheat, triticale, rice, alfalfa, tomato, soybean, perennial ryegrass, snapbean, cotton, maize, rye, sunflower, pea and sweet potato (Foy, 1974; 1983a). Reports of differential tolerances to manganese within plant species include wheat, apple, triticale, soybean, cotton and flax (Foy, 1983a).

The existence of such differences has raised the possibility of breeding, within agriculturally important plants, for improved tolerance

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to soil acidity. These differences have been extensively and frequently reviewed (Wright and Ferrari, 1976; Foy and Fleming, 1978; Foy, 1984), with emphasis on the physiological and biochemical basis for toxicity (Haug, 1984) and tolerance, particularly with reference to aluminium.

Views diverge widely on the role of plant tolerance in the restoration of productivity on acid soils. Some authors enthusiastically endorse the usefulness of tolerance (e.g. Vose, 1981; 1983; Frey, 1985), while others express doubts. Fox (1980) describes the use of tolerance as like 'the hazard of flying a low-powered aircraft up a narrow canyon. The course starts easily and the scenery is beautiful, but options run out very quickly and to continue is to invite disaster'. Such a view seems to envisage tolerance as an alternative to liming. In this chapter we have explored the relationship between liming and plant tolerance to acidity.

We believe that using the plant's tolerance to acidity is an important, complementary approach to soil amendment (e.g. liming) and this is particularly true in the extensive agriculture practised in most of Australia. The adoption of liming is limited by its high cost in an agricultural system which has relatively low cost inputs and low profitability per hectare. Using crops tolerant of acid soils may prove to be an essential aspect of management of soil acidity as in South America (Sanchez and Salinas, 1982). Indeed, it has been suggested that sensitivity to mineral stress in the wheat and rice cultivars of the 'green revolution' may have been a major shortcoming in the adaptation of these cultivars (Foy, 1983a).

In this review we emphasise several areas of interest which have not been reviewed recently. We aim to meet the information requirements of a plant breeder attempting to produce cultivars more tolerant of soil acidity. We use examples relevant to temperate Australian agriculture with emphasis on cereals, partly because much is known about these species and partly because this is the area in which the authors are actively involved.

II. TOXICITY SYMPTOMS AND TOLERANCE MECHANISMS

A. Aluminium

1. Toxicity

The effects of aluminium are primarily on the root system, causing reduced root elongation and, at high aluminium levels, the death of the growing point. The lateral roots appear to be more sensitive to damage than primary roots but all root growth is damaged as aluminium levels are increased. This gives the typical 'stubby root' appearance with few, fine-branching roots. As a result the root system is inefficient in absorbing nutrients and water.

However, symptoms of aluminium toxicity in tops are reasonably diverse and not easily identified. This is not surprising as aluminium interferes with the uptake, transport and use of essential elements such as calcium, magnesium, phosphorus, potassium and iron (Foy, 1983b) and an aluminium-induced deficiency of any of these elements may affect the symptoms shown.

The effects of aluminium toxicity on root elongation and death of the growing point are rapid, occurring in a matter of hours. This observation on roots is the basis of many of the rapid tests for aluminium tolerance in plants.

2. *Tolerance*

Tolerance to aluminium can operate by preventing or reducing aluminium uptake by plants or by detoxifying aluminium once it is in the plant tissue. Exclusion of aluminium from the plant may operate in several ways.

First, the pH in the root zone may be increased and this decreases the solubility and toxicity of aluminium. This process involves the plant accumulating more anions than cations and excreting hydroxyl ions or Bronsted-Lowry bases (Helyar, 1978). This process has been demonstrated in wheat (Foy and Fleming, 1978; Fleming, 1983). Varieties of wheat tolerant of aluminium tended to increase the pH of the nutrient solution in which they were grown while aluminium-sensitive varieties lowered the pH. The mechanism appeared to be that tolerant plants were able to take up some nitrate in the presence of ammonium while sensitive plants took up relatively more ammonium.

Second, low cation exchange capacity of the roots has been suggested as being associated with aluminium tolerance (Vose and Randall, 1962). This would be expected to reduce the diffusion of trivalent aluminium and also to reduce the severity of the effects of aluminium on cell wall expansion as there would be fewer, free carboxyl radicals in cell walls to which the aluminium could bond (Helyar, 1978).

Third, some resistance by the plasmalemma to aluminium damage has been suggested. This would then restrict aluminium diffusion into the cytoplasm (Henning, 1975; Foy, 1983b).

Fourth, morphological change under aluminium stress has been suggested as a mechanism for tolerance (Hecht-Buchholz and Foy, 1981). These authors suggested that a mucigel was produced to protect the root from aluminium damage. Hecht-Buchholz (1983) has reviewed morphological damage and adaptation to a range of mineral deficiencies and toxicities.

Once aluminium has penetrated the plant tissue, other tolerance mechanisms may operate. First, in certain woody species and in

'accumulator' species, cytoplasmic aluminium is complexed by organic molecules and so does not disrupt the cell metabolism (Jones, 1961; Jackson, 1967). This aluminium, once inactivated, may be held in the cytoplasm or deposited in old xylem vessels or cell walls (Helyar, 1978). The detoxification of aluminium by tea (*Camellia sinensis* L. Ktze), an aluminium accumuluator, appears to be accomplished by this mechanism (Sivasubramaniam and Talibudeen, 1972; Memon *et al.*, 1981).

The importance of this internal tolerance in distinguishing between genotypes of a species is unclear. It may be unimportant in the broad range of agricultural plants, although some examples of a relationship between tolerance and aluminium accumulation in tissue can be found in the literature. Differential internal tolerance has been reported with rye (Aniol *et al.*, 1980), snapbean (Naidoo, 1976) and in the callus cell cultures of tomato (Meredith, 1978a,b).

Second, differential distribution of tissue aluminium between tops and roots has been reported as a possible tolerance mechanism (Foy, 1983b).

Third, as aluminium disrupts the uptake, transport and use of a range of essential nutrient elements, 'efficiencies' in uptake or utilisation of nutrients have been suggested as negating the disruptive effect of aluminium toxicity. In potato and maize, magnesium uptake was greater in varieties tolerant of aluminium toxicity than in sensitive varieties (Foy, 1983b). The ability of plants to tolerate low internal concentrations of calcium, phosphorus and iron have been suggested as the basis for aluminium tolerance (Baumgartner *et al.*, 1976; Foy and Fleming, 1978).

B. Manganese

1. Toxicity

Manganese toxicity primarily affects plant tops rather than roots and produces specific symptoms in the tops of some species. With soybean grafts, Heenan and Carter (1976) reported that the genotype of the scion determined the response to manganese toxicity. However, with alfalfa genotypes, Ouellette and Dessureaux (1958) concluded that the genotype of the root determined the response.

The most common symptom of manganese toxicity is the chlorosis of leaf tip and margins followed by necrosis, particularly on the older leaves. This can be accompanied by chlorotic or necrotic flecking or mottling on the leaf margins or whole leaf. Under greater stress the symptoms appear on progressively younger plant tissue. 'Puckering', 'crinkling' or 'cup-

ping' has been described in soybean (Heenan and Carter, 1977), and for a range of crops including cotton, rape, kale, lettuce and snapbean (Foy, 1983b).

Generally the damaged plant tissue (i.e. leaf margins, interveinal spots or flecks on older tissue) has a higher concentration of manganese than the surrounding tissue. This accumulation appears to be due to low phloem mobility of manganese which leads to manganese accumulation at the extremities of the xylem system (leaf margins and interveinal leaf tissue; Vlamis and Williams, 1973). Interveinal chlorosis has been shown to be due to manganese-induced iron deficiency in some but not all instances (Hewitt, 1963).

Browning of roots has been reported in nutrient cultures high in manganese (Morris and Pierre, 1949; Foy, 1983b). E. A. Polle (pers. comm.) drew attention to a symptom of 'banding' on the roots of seedling wheat grown in dilute solutions of manganese. This symptom was reported in 1927 (Barton and Trelease, 1927). In Polle's experience and ours, the appearance of this symptom was not related to manganese tolerance although varieties did vary in their reaction, from no apparent effect to a clear 'banding' (see Fig. 1).

Helyar (1978) has noted the role of manganese as a cofactor in the activity of many enzymes and has suggested that plant damage with high concentrations of manganese in tissues is due to loss of control of at least some of these enzymes activated by manganese. Manganese has a role in phosphate transfer reactions, the Krebs cycle, a number of oxidases, nitrate reductase and in photosynthesis.

Effects of manganese toxicity on some of these processes have been noted (Sirkar and Amin, 1974; Aoba *et al.*, 1977; Scott, Burke and Bostrom, 1987). The circumstantial evidence, then, is that effects of manganese toxicity on these plant functions are likely to be the primary damage to the plant. However, with such a diverse set of sites for metabolic disruption under manganese stress, it is likely that secondary effects occur and that the concentrations of many metabolites are likely to differ from the normal level.

2. *Tolerance*

Plant tolerance to high levels of soil manganese may operate by exclusion, by restriction of manganese transport to plant tops, and by tolerance of shoots to high internal concentrations of manganese.

Exclusion of manganese as a tolerance mechanism may improve plant performance in a manganese-toxic soil but would also make the plant more susceptible to deficiency in other situations. There is

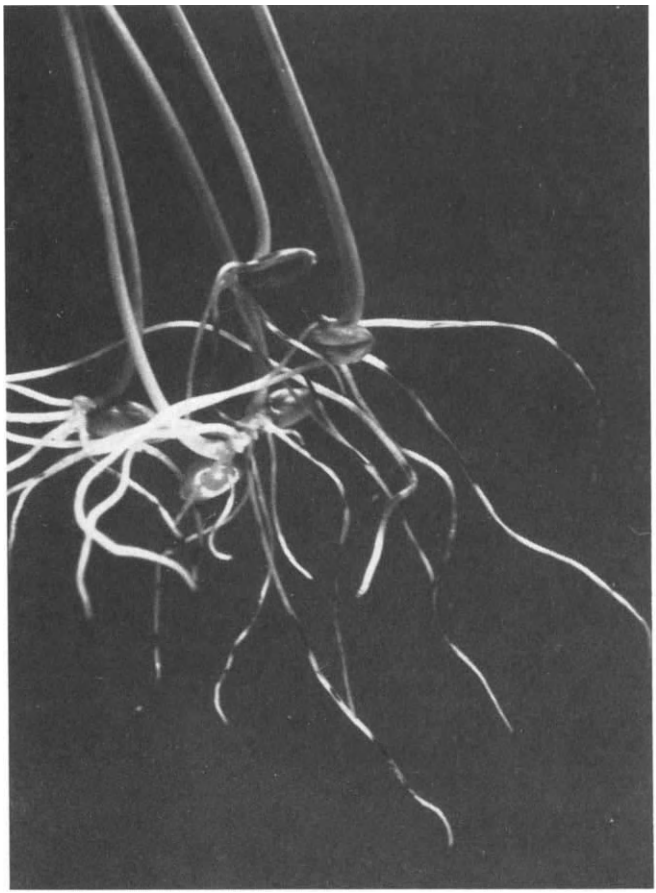


Fig. 1. Clear 'banding' in the roots of the Brazilian cultivar. Carazinho, four days after germination and growth in a dilute solution (0.2 mM) of manganese chloride. Similar results were obtained with manganese sulphate solutions.

evidence of this mechanism operating among species and some evidence of differential uptake at a cultivar level (Helyar, 1978).

Restricted movement of manganese from roots to tops has been suggested as a basis of tolerance in lucerne (Ouellette and Dessureaux, 1958), and a range of other species (Andrew and Hegarty, 1969; Robson and Loneragan, 1970; Edwards and Asher, 1982). Such a mechanism proposes that manganese can be isolated or 'inactivated' in the root and that this does not damage the root. For example, some key metabolic pro-

cesses (e.g. photosynthesis), disrupted by high levels of tissue manganese, occur in the tops rather than in the roots.

Tolerance to high levels of manganese in shoots may be the major mechanism operating in a wide range of species. Heenan and Carter (1976), in a grafting experiment with soybean, demonstrated that tolerance was related to the genotype of the shoots rather than the genotype of the roots. Edwards and Asher (1982) thought this was the most important mechanism for manganese tolerance shown by a wide range of species tested by them. However, the first two mechanisms were also operating. Similar conclusions were reached by Temple-Smith and Koen (1982) with a range of crop types and by Smith (1979) with a group of tropical grass species.

At the level of cultivars within a species, tolerance to manganese in shoots has been reported as important in soybean (Brown and Devine, 1980; Heenan and Campbell, 1981), wheat (Foy *et al.*, 1973; authors' unpublished data), cotton (Foy *et al.*, 1981), siratro (*Macroptilium atropurpureum*, Hutton *et al.*, 1978) and cowpea (Horst, 1980; 1983).

The basis of tissue tolerance to manganese has been attributed to: (1) the formation of metabolically inactive, organic manganese complexes (Foy, 1984); (2) binding to cell walls and/or deposition in vacuoles (Helyar, 1978); and (3) tolerance by some vital enzyme systems of high concentrations of ionic manganese (Scott, Burke and Bostrom, 1987).

Localisation of manganese in plant tissue has been described by Memon *et al.* (1980), who noted that the highest concentrations of manganese occurred in the epidermis, collenchyma and bundle sheath cells in the manganese-accumulator species *Acanthopanax sciadophylloides*. Foy (1984) has suggested that this localisation may be a tolerance mechanism that keeps manganese from key metabolic sites. By contrast, Horst and Marschner (1978) and Horst (1983) ascribed the greater manganese tolerance of beans, when silicon was added to solutions, to the more homogeneous distribution of manganese in the leaf. High concentrations of manganese in local areas of leaf were associated with symptoms of brown spots.

III. TOLERANCE AND LIMING

Concern is expressed that the introduction of a range of tolerant cultivars would negate the need for liming and, in acidifying agricultural systems, acidity problems would intensify unchecked. We believe this view is based on reports in the literature of the non-response of tolerant cultivars to lime application (Martini *et al.*, 1977). In this study there was no response to liming for 19 Brazilian wheat cultivars tolerant of aluminium

toxicity (mean yield 2110 kg. ha^{-1} when unlimed, 1820 kg. ha^{-1} when limed) compared to the response of 49 cultivars from a range of other countries (mean yield 570 kg. ha^{-1} when unlimed, 1210 kg. ha^{-1} when limed).

There are, however, other data in the literature, which indicate that the relationship between tolerance to aluminium and response to lime is frequently different from this. In fact, in another study reported by Martini *et al* (1977), increased grain yield in a tolerant cultivar of Brazilian wheat (IAS-52) is reported following liming. We believe that the broader evidence indicates that both liming and tolerance have a role to play in increasing production from acid soils. A range of such views has been discussed by Foy (1983a).

In order to consider the relationship between tolerance and lime use, it is necessary to describe the responses of a tolerant and a sensitive cultivar to the application of lime.

A. Relationship of tolerance and response to lime — a proposed model

The proposed model is illustrated in Figure 2. A serious aluminium problem is corrected by liming. The points marked A to D on this figure

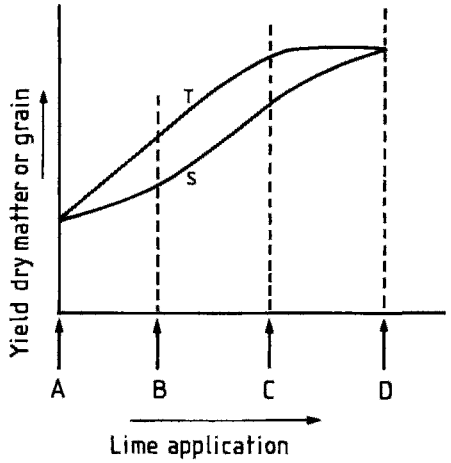


Fig. 2. The idealised response to lime application by an aluminium tolerant (T) and a sensitive (S) cereal cultivar grown in a soil with toxic levels of aluminium. At point A aluminium toxicity limits both tolerant and sensitive cultivar; at point B the tolerant cultivar outyields the sensitive cultivar; between B and C both cultivar react similarly and between C and D the tolerant cultivar does not respond but the sensitive cultivar does.

are described here. At point A there is a serious aluminium toxicity which restricts the growth of both the tolerant and the sensitive cultivar. When lime is applied, the tolerant cultivar gives a greater response up to point B, but the sensitive cultivar shows little or no response. Between B and C both cultivars react similarly i.e. the yield increase (dry matter or grain) is the same in absolute terms. Tolerance here results in higher yield but not in a differential response by the cultivars. Between C and D the tolerant cultivar does not respond to further lime application but the sensitive cultivar continues to respond. D is the point at which aluminium toxicity is removed from the plant root environment of both cultivars and in this example the cultivars have been assumed to give the same yield under these circumstances.

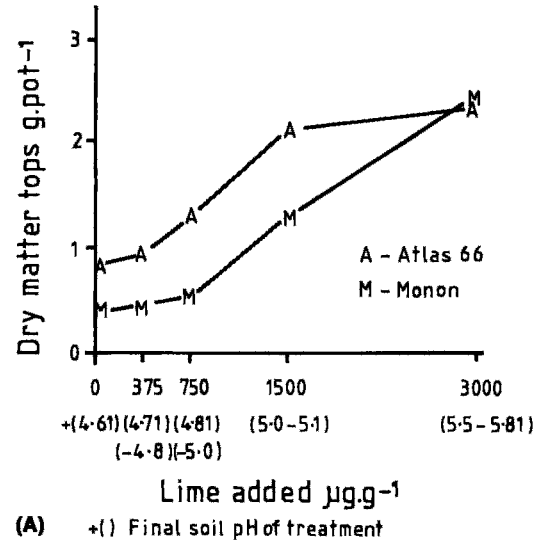
The above description is based on absolute yield and if ratios of yield (nil or low lime/high lime) are used to correct for yield differences between cultivars, the essential features of the model are obscured. We suggest that ratios are inappropriate as they appear to show the sensitive as more responsive only because of their lower yield under stress. Liming beyond point D may give yield reductions under some circumstances and again ratios need to be interpreted with care.

This model would apply where aluminium toxicity was the dominant factor limiting yield and cultivars were reasonably adapted to the area. If these conditions are not met, low yields may be due to factors other than aluminium sensitivity. We were unable to find data on which to base a model for liming, manganese toxicity and manganese tolerance.

B. Evidence in support of the model

This model is supported by some examples from experiments using wheat and barley (Fig. 3). The data presented describe the responses to liming of tolerant or sensitive cultivars of wheat and barley in experiments in pots ('Bladen' and 'Tatum' soils) and in the field. The aluminium tolerances referred to have been determined independently of these results.

In a pot experiment using the aluminium toxic 'Bladen' soil (Foy *et al.*, 1973), the responses of the wheat cultivars Atlas 66 (aluminium-tolerant) and Monon (aluminium-sensitive) to liming were determined (Fig. 3A). The range of approximately parallel response (B to C, Fig. 2) is apparent in the range from nil lime to 1500 $\mu g.g^{-1}$. The range of non-response of the tolerant and continued response of the sensitive (C to D) is present in the range between 1500 to 3000 $\mu g.g^{-1}$ of lime. At the highest rate of lime the plants would probably not be exposed to an aluminium stress.



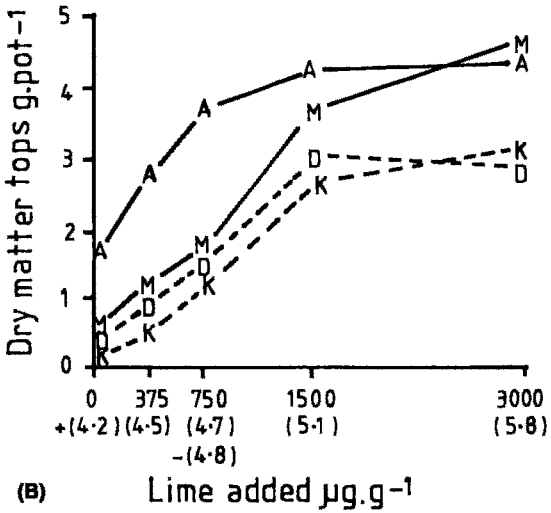
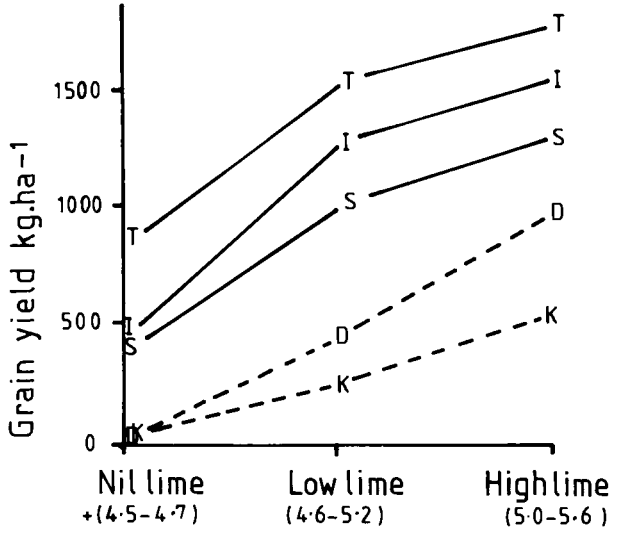
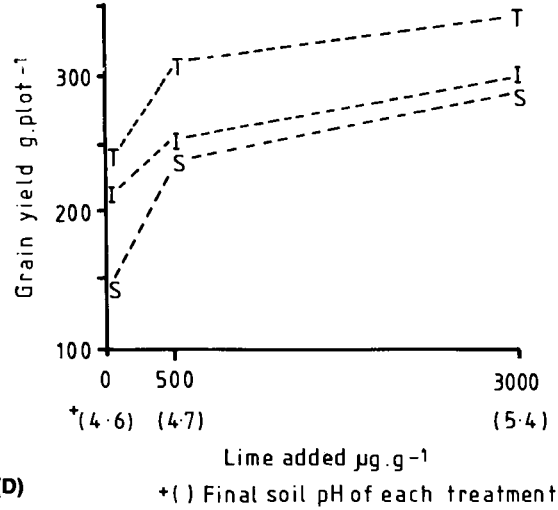


Fig. 3.(A) Response in dry matter yield by the wheat cultivars Atlas 66 (A; aluminium tolerant) and Monon (M; aluminium sensitive) to the application of lime. Plants were grown in a pot experiment using aluminium toxic 'Bladen soil; (after Foy *et al.*, 1973).

(B) The response in dry matter yield by wheat and barley to lime application.Plants were grown in pots using aluminum toxic 'Tatum' soil. The wheat cultivars (solid lines) were Atlas 66 (A) and Monon (M) and the barley cultivars (broken lines) were Dayton (D; aluminium tolerant) and Kearney (K; aluminium sensitive); (after Foy *et al.*, 1965).



(C) +( ) soil pH range over sites and years for each lime treatment.



(D) +( ) Final soil pH of each treatment

(C) Effects of lime on grain yield in the field, averaged over three seasons, for wheat (solid lines) and barley (broken lines). The wheat cultivars were grouped, (as described in the text) into a tolerant group (T) , a sensitive group (S) and a group with intermediate reaction (I) to high aluminium. The barley cultivars are Dayton (D) and Kearney (K); (after Lafever *et al.*, 1977).

(D) Effects of lime application on the grain yield of barley cultivars in the field in one season. The barley cultivars have been grouped on the basis of a greenhouse pot experiment into the 10 most tolerant of aluminium (T) , the 10 most sensitive (S) and the remaining 10 intermediate lines (I); (after Reid *et al.*, 1969).

In another experiment conducted in pots using the aluminium-toxic 'Tatum' soil (Foy *et al.*, 1965), Atlas 66 and Monon wheat were again tested as well as the barley cultivars Dayton (aluminium-tolerant) and Kearney (aluminium-sensitive). Results for both the wheat and barley cultivars (Fig. 3B) were similar to those presented in Figure 3A. The higher rates of lime applied in this experiment depressed yields.

In the same paper (Foy *et al.*, 1965), the two barley cultivars were grown on the 'Bladen' soil. Liming increased dry matter production per pot by Dayton from 2.8 to 3.2 g and increased that by Kearney from 0.4 to 0.5 g. We believe that this illustrates the range A to B in Figure 2, as the lime rate used was low and the '+ lime' treatment only attained pH 4.7 (method not stated). Compared to Kearney, the yield of Dayton was higher and its yield response to liming was greater in absolute terms.

Lafever *et al.* (1977) reported responses of cereal grain yields to liming in the field (Fig. 3C). The 23 cultivars of wheat (the authors' group 1) have been split into three classes based on the results of the solution culture tests reported in the same paper. The seven cultivars which were most aluminium-tolerant in solution culture were grouped as the tolerant group (T). The seven most sensitive were grouped (S) and the remaining nine formed the intermediate tolerance group (I). The grain yield data were averaged over three seasons and, as the experiment was not on the same plots each year and lime was applied at different rates, the pH ranges of the surface soil are given and the 'low' and 'high' lime nomenclature is used.

We believe that the section B to C of Figure 2 is illustrated in the wheat yields (Fig. 3C). All groups responded similarly to liming and tolerance was an advantage irrespective of liming treatment at this site. Aluminium toxicity was not eliminated and the authors emphasise this point. The sub-surface soil was acid and so surface liming did not ameliorate aluminium toxicity in the rooting profile of the crop. In other words point D of Figure 2 (no aluminium toxicity) was not attained.

Correlation coefficients between an independent measure of aluminium tolerance for each wheat cultivar (the ratio of root length at nil aluminium to root length at 8 $\mu g.mL^{-1}$ of aluminium in solution) and the grain yield in the field for nil, low and high lime rates were calculated from the data given by Lafever *et al.* (1977). The coefficients were 0.68, 0.69 and 0.62 respectively and all were significiant ($p < 0.01$). Clearly, tolerance to aluminium was associated with higher grain yield in the field even when high rates of lime had been applied.

At 'high' rates of lime, the sensitive group produced 345 per cent of the yield achieved when no lime was applied. Similarly, the tolerant group produced 217 per cent of the yield achieved when no lime was

applied. The sensitive cultivars then appear to be more responsive, but in fact the absolute increase in yield was 956 $kg.ha^{-1}$ for the sensitive group and 959 $kg.ha^{-1}$ for the tolerant group. The tolerant group then was equally responsive, in terms of absolute yield increases, and the tolerant group had the higher yield at all lime rates. Using ratios to compare yields at high lime with those at nil lime is misleading.

In the same experiment (Fig. 3C), the yield of the barley cultivar Dayton (aluminium-tolerant) increased more than that of Kearney (aluminium-sensitive) and matched the range A to B in Figure 2. Compared to the wheat cultivars which covered the range B to C, the barley was under a greater stress. We suggest that this is due to the greater sensitivity of barley to aluminium. The response of these barley cultivars is an example of greater response by an aluminium-tolerant cultivar to lime application compared to the response from a sensitive cultivar.

Reid *et al.* (1969) reported the response of 30 cultivars of barley to liming in the field. Their grain yields are given in Figure 3D with the barley cultivars grouped into the 10 most tolerant of aluminium (T), the 10 intermediate (I) and the 10 most sensitive (S) lines. The basis of this grouping is the tolerance ranking (yield at low lime to yield at high lime), reported in the same paper, from a greenhouse experiment using an aluminium-toxic soil. This tolerance index correlated well ($r = 0.92$; $p < 0.001$) with that obtained for 13 of the lines in a subsequent solution culture experiment (Reid *et al.*, 1971), in which the index used was root length at nil aluminium/root length at 8 $\mu g.mL^{-1}$ aluminium.

All tolerance groups responded to lime application (Fig. 3D). The sensitive cultivars gave a greater increase in yield than the tolerant cultivars (98 $g.plot^{-1}$ cf. 51 $g.plot^{-1}$). The data are in the range B to greater than C in Figure 2. Aluminium toxicity was probably not eliminated at this site as the tolerant group out-yielded the sensitive group even at the high lime rate. A significant correlation ($r = 0.39$; $p < 0.05$) was present between the tolerance index derived in the greenhouse (described above) and absolute grain yield in the field at the high lime rate, suggesting that the plants were still experiencing aluminium toxicity.

C. Implications and discussion of the model

It should not be expected that sensitive cultivars will always be more responsive to liming than tolerant ones. The responsiveness will vary with the initial soil condition and the extent to which that has been changed by liming, as well as the relative tolerance range of the cultivars being tested. In some situations (Fig. 2, A to B) liming may only be

economic if a tolerant cultivar is used. In all other situations a tolerant variety will exceed or equal the yield and hence the economic return obtained from growing a sensitive cultivar.

It is our experience in New South Wales that tolerance to acid soil conditions can play an important role as a component of acid soil management. In two situations on acid soils (Doyle and Bradley, 1982; Scott, 1982) higher yields were obtained with tolerant cereals than with sensitive cereals. Additionally both tolerant and sensitive cereals responded to liming. In practice, the complete elimination of acidity from a soil profile, for the duration of crop growth, is a situation which is difficult to achieve for a number of reasons.

First, we have already drawn attention to acidity in the profile which is below the depth of lime incorporation. Second, variability of the acidity problem across a site results in insufficient lime being applied in some very acid areas following treatment at a single lime rate. Third, poor spreading or incorporation of lime may leave areas or portions of soil unlimed. Fourth, liming just prior to sowing may leave young plants exposed to an acidity stress as the reaction of lime with the soil may be incomplete. Finally, the farmer's practice of 'hedging' or reducing fertilizer rates to less than those recommended may leave acidity problems only partially amended. The variability problems are described in greater detail in Chapter 6 this monograph.

Using ratios of yield with and without lime to compare cultivars of varying tolerance obscures these economic implications of tolerance. Ratios can be used as an index of tolerance only if liming produces point D in Figure 2 and the cultivars show a range of responses under the stress. If point D is not achieved then the ranking of cultivars will depend on the range of stress covered.

IV. BREEDING FOR TOLERANCE

A. Requirements for breeding

A frequently quoted example of successful breeding for tolerance is that of wheat breeding in Brazil. Since 1919 in that country, breeders have selected and later bred wheat for tolerance to 'crestamento', a leaf 'burn' condition in wheat (Da Silva, 1976). In retrospect it appears that selection in this way was for tolerance to soil acidity, in particular to aluminium toxicity. While such an experience shows what is possible in breeding for tolerance, the breeding was done on an *ad hoc* basis. Devine (1976) has listed the techniques and information required for the formulation of a deliberate breeding program. These requirements are

that: (1) techniques are available for identifying tolerance; (2) there is a reasonable range of variability within the species; (3) the character is heritable and some estimate of heritability is available; (4) there are no strong, undesirable genetic correlations with tolerance; (5) an estimate can be made of the level of improvement attainable in the field.

It is generally acknowledged that these requirements need to be met by plant nutritionists, biochemists, physiologists and others before plant breeders will be able or motivated to undertake planned breeding programs aimed at the regular production of improved, acid-tolerant cultivars. While much has been achieved in this direction, crops and pastures with greater tolerance to soil acidity remain, in general, a promise yet to be fulfilled.

While claims have been made of tolerance to acid soil by species and cultivars, these claims are based on field observations rather than being the result of a conscious breeding effort. At Wagga Wagga in southern New South Wales, we are committed to a project on the breeding of a wheat cultivar tolerant of acid soils (Fisher and Scott, 1983). We are not alone as Mexican workers, cooperating with other workers In Brazil, have already produced aluminium-tolerant lines for further testing (Anon., 1984).

B. Screening for tolerance

There are three stages of selection in a breeding program, and the requirements of a test for tolerance differ in these stages.

The first stage is identifying parental lines. Tests at this stage must be precise and frequently multiple tests would be used, often in series, to finally identify the best parental lines. In our program at Wagga Wagga, three tests are used in sequence, a rapid laboratory test, growing plants in nutrient solution and finally testing the lines in field trials. In the final choice of parental lines, it is not essential to be able to test large numbers of lines. Field trials are used, not only to confirm the tolerance of the chosen lines, but also to identify faults in the cultivars which may need correction in the breeding program. If different tolerance mechanisms exist, a knowledge of the basis of tolerance in a particular cultivar would be useful and may allow different types of tolerance to be combined. Hopefully, different tolerance mechanisms combined in this way would be additive.

The second stage of selection is testing in segregating populations. The requirements of the selection test will depend on the aim and methods of the breeding program. At one extreme, if the aim is to move one dominant gene from a tolerant cultivar to an otherwise well adapted

cultivar, then the population size required would be small (20 plants per generation) and relatively slow tests would be adequate. At the other extreme, where inheritance is complex and it is necessary to seek improvement in other characters simultaneously, it will be essential to screen many thousands of plants. This latter case is the more common in plant breeding, so it is desirable that a selection test be very rapid. Sometimes a less precise test may be acceptable if it allows a larger population to be handled. In this case the selected population would need to be retested with a more precise test. In backcrossing or complex crosses, where the selected line is to be used immediately in the crossing program, it is essential that the results of testing are available before the end of flowering.

The final stage of testing is confirmation that the selected lines perform as required. The requirements at this stage are similar to selecting parental lines. Rapidity of tests is not as important as precision. It is essential to do field tests in the environment in which the cultivar will be grown.

Plants may be screened for their tolerance to acid soil conditions by testing in soil either in the field or glasshouse. Alternatively sand or solution culture systems can be used. All of these approaches have their advantages and disadvantages.

1. Field screening

Field screening has been the basis of the success of the Brazilian wheat breeding effort. The testing relied on the presence or absence of the condition known as 'crestamento'. This condition is described as causing premature death in severe situations (Da Silva, 1976) but is more usually described as a leaf 'burn' with associated poor root development and 'underdeveloped, yellow-green plants with short, thin stems and narrow leaves' (Martini *et al.*, 1977). Campbell and Lafever (1976) also drew attention to the stunting of wheat on acid soils and suggested that differential stunting could be used to separate lines which differed greatly in their tolerance.

Howeler and Cadavid (1976) have successfully screened rice in the field for tolerance but found better differentiation of their lines when they used a low rate of lime, suggesting that the unamended soil was too acid relative to the range of tolerance available in their material. Their selection criterion was absolute grain yield in the field.

Kang and Fox (1980) used lime and sulphur and/or sulphuric acid to establish a pH gradient on a manganiferous oxisol. Cowpea (*Vigna unguiculata*) cultivars were sown along the pH gradient with the aim of

testing cultivars for their manganese tolerance. They were able to establish tolerance differences by this 'continuous function experimental design'.

The testing of tolerance in this way evaluates plants in the soil and climate in which they are to be grown commercially. The disadvantages of field testing are: the time taken (usually one growing season); problems of soil variability; the confusing effects of differential resistances of material under test to diseases and pests; and the vulnerability of the material to environmental hazards such as drought, flood and lodging (Howeler and Cadavid, 1976). All of these factors may make tolerance to a soil factor difficult to identify with certainty and precision.

2. Glasshouse screening with soil

Studies here can be divided into two types: (1) those which use a problem field soil; and (2) those in which the soil is used only as a screening medium and is not directly associated with the acidity problems under study.

The soil in category 2 is chosen carefully to produce either aluminium or manganese toxicity in the species to be evaluated. The approach is that of a screening test and not that of studying a field problem in the glasshouse.

Surprisingly few studies fall into the first category. Some examples would be those of Mugwira *et al.* (1978), Camargo and Oliveira (1981), Long *et al.* (1973) and Culvenor *et al.* (1986a). The advantage is that plants are screened for their suitability on a relevant soil, i.e. while it may be suggested that aluminium or manganese toxicity is involved, a precise diagnosis of the problem, while helpful, is not essential.

The use of soil as a screening medium for aluminium and manganese tolerance has been discussed by Foy (1976). Andrew (1976) has outlined the use of soil as a medium for screening for manganese tolerance in legumes. The problems are those of producing a toxicity of the correct type and of a magnitude appropriate to the range of tolerances under test. The soil chosen should produce a single stress of either aluminium toxicity or manganese toxicity, which does not interact with other nutritional deficiencies (e.g. calcium, phosphorus, molybdenum, magnesium).

The problem with a soil as a screening medium is variability caused by the site of collection itself, time of collection and storage conditions for the soil (particularly with manganese). The stress chosen can be obtained by acidifying a soil, liming or adding manganese. Additions of basal nutrients are aimed at preventing nutrients other than the desired

stress from affecting growth. In practice, experience is required both with the soil and with the plant species being tested, and care is needed in the interpretation of results. Using cultivars of known reaction to the planned toxicity in each experiment is an advantage.

Despite these precautions, Foy (1976) points to surprising results in some experiments and gives examples of molybdenum deficiencies and combined aluminium and manganese toxicities operating in some experiments where aluminium stress alone was planned.

3. Screening with nutrient solutions

The advantage of solution culture experiments in research on plant tolerance to aluminium and manganese is that greater control can be exerted over the level of exposure to the toxic element, the level of other nutrients in the solution and pH.

The major concern is that the rankings for tolerance in solution culture cannot be reproduced in a soil of the same toxicity. For this reason there are numerous papers which document cultivar tolerance in both a solution culture system and in a pot experiment using soil. Examples for aluminium tolerance are in barley (MacLeod and Jackson, 1967; Reid *et al.*, 1971), wheat (Foy *et al.*, 1965), rice (Nelson, 1983), soybean (Sartain and Kamprath, 1978) and sunflower (Foy *et al.*, 1974). Similar research has been conducted on manganese tolerance e.g. in triticale (Mugwira *et al.*, 1981), wheat (Foy *et al.*, 1973) and cotton (Foy *et al.*, 1969). The general thrust of these papers is that solution culture results gave similar cultivar rankings to those obtained in soil. However some variability has been reported (Foy, 1976) and may be due to the greater availability of nutrients such as phosphorus in nutrient solutions compared to availability in a soil, particularly to a plant with a root system damaged by aluminium toxicity.

However, there are several factors (particularly those related to the control of the toxic element stress imposed) which need to be considered to ensure a successful solution culture experiment.

a Aluminium: The factors controlling the solubility and speciation of aluminium in solution are discussed in detail in Chapter 1 of this monograph. The pH and concentration of phosphorus in solution should be low in order to impose and control the aluminium stress. It is necessary to control these factors either by frequent monitoring and adjustment and/or by frequent solution changes. Flowing culture systems which require only low phosphorus levels in solution for plant growth and have continuously monitored pH are ideal but complex. The control

of nitrate and ammonium concentration offers some scope for stabilising the solution pH.

The level of calcium and magnesium in solution can also influence the severity of aluminium toxicity. This has been exploited by Rhue and Grogan (1977), who varied the calcium and magnesium in solution to control the plant damage caused by a constant aluminium level. A comprehensive approach to the design of a short-term (14 to 17 days) screening system for testing aluminium tolerance in sorghum has been described by Furlani and Clark (1981). These authors varied concentrations of aluminium, calcium, potassium, magnesium and phosphorus, source of nitrogen (nitrate, or ammonium, or a combination of both) and temperature regime in establishing levels of each for a screening test. High phosphorus, calcium or magnesium protected the plants against aluminium damage. Potassium level, in the range tested, had no effect on severity of aluminium toxicity, and plant damage by aluminium increased with increasing temperature in the range (day/night) of 23/18 to 33/28°C. Increasing the temperature during both day and night from 5 to 35°C also increased plant damage (Aniol, 1983).

b Manganese: The expression of manganese toxicity can be altered by a number of factors, other than the level of manganese in solution. These factors need to be controlled in order to separate reliably cultivars or species on the basis of their manganese tolerance.

Increased concentrations of calcium, magnesium, and ammonium in solution as well as lowered pH decreased the uptake of manganese by plants (Jackson, 1967; Robson and Loneragan, 1970; Heenan and Carter, 1975; Shuman and Anderson, 1976; Osawa and Ikeda, 1980). The beneficial effects of ammonium may be due partly to the lowering of external pH when plants absorb ammonium (Foy, 1983b). An increase in phosphate in solution has been reported as increasing manganese uptake and toxicity (Foy, 1983b).

Increasing temperature appears to increase uptake of manganese by plants but also enhances the plant's tolerance of high levels of tissue manganese. These effects have been reported for soybean (Heenan and Carter, 1977), tobacco (Rufty *et al.*, 1979) and rice (Nelson, 1982).

Addition of silicon to nutrient solutions has been found to alleviate manganese toxicity in barley (Williams and Vlamis, 1957), grasses (Vlamis and Williams, 1967) and beans (Horst and Marschner, 1978; Horst, 1983). This effect appears to be due to a more homogeneous distribution of manganese in the leaf tissue rather than to lower manganese concentrations. Silicon prevented the accumulation of manganese in local areas of the leaf, which otherwise resulted in necrotic

spots (Horst and Marschner, 1978). However there is also some evidence of silicon reducing manganese uptake (Foy and Fleming, 1978; Foy, 1983b).

4. Rapid screening

Soil or solution culture studies, taking 4 to 8 weeks to complete, are generally used in experiments on aluminium tolerance in plants. However, the development of more rapid laboratory or glasshouse screening techniques for the detection of tolerance offers many benefits. The search for improved tolerance is easier as more material can be screened, and heritability studies can be more comprehensive. From the plant breeder's viewpoint, such rapid testing enables large numbers of breeding lines or individual plants to be tested routinely.

In all rapid laboratory tests for aluminium tolerance, the basis for predicting plant performance in soil is the effect of aluminium on roots over a short time span. The correspondence between the two is acceptable in general terms only (Reid *et al*, 1971; Campbell and Lafever, 1976; Howeler and Cadavid, 1976). Sartain and Kamprath (1978) drew attention to some lack of agreement between ranking of soybeans for aluminium tolerance in a soil experiment in pots and a short-term assessment of root growth. They noted that the short-term studies of root elongation accounted for the effects of aluminium on cell elongation and cell division while the pot experiment integrated many other effects over a longer time. These included the continued effect of aluminium on top and root growth and nutrient uptake. Hanson and Kamprath (1979) reported similar experiments and noted that some expressions of seedling tolerance do not carry over as tolerance in adult plants.

In most rapid tests, root length is measured (or estimated) and compared with a control at nil aluminium. Such methods have been described for wheat by Campbell and Lafever (1976) and Kerridge *et al.* (1971), for barley by Reid (1976), Kaminska (1981) and McNeilly (1982), for phalaris by Culvenor *et al.* (1986a) and for a range of crops by Konzak *et al.* (1976) and Mugwira *et al.* (1978).

These methods are most successful when the treatment and the nil aluminium control can be run concurrently. This may only be possible when testing the tolerance of established cultivars in self-fertilizing species. In cross-pollinating species the variability within a cultivar increases the experimental variability. When segregating breeding material is used, it is not possible to run a nil aluminium control, although the parents of the cross may be tested.

If it is not possible to run a concurrent control, the experiment should be run for a relatively long time so that slow root growth due to other

factors is not confused with aluminium sensitivity (e.g. Reid, 1976 for 18 days; McNeilly, 1982 for 13 days). The disadvantage of these systems is that they must be maintained with frequent pH corrections and a decision must be made either to include or exclude phosphorus. In some systems, however, the pH is only adjusted at the beginning of the test (e.g. Mugwira *et al.*, 1978) and in others only aluminium is added to the solution, and no nutrients are present (Kaminska, 1981).

With wheat, a number of rapid tests have been developed. The most convenient is that using a haematoxylin stain (Polle *et al.*, 1978). This test can demonstrate aluminium tolerance in four-day-old seedlings and therefore with such small plants minimal space is required. Because of the short duration of the test, no phosphorus is required. The haematoxylin stain test, with some modifications, is successful with other species. This strategy — the testing of young seedlings — is needed in other crop and pasture species and for other mineral stresses (e.g. manganese tolerance). No test is available for the rapid evaluation of manganese tolerance in cereals.

At Wagga Wagga we are developing a test for aluminium tolerance which has some features in common with that of Polle *et al.* (1978). It is an enhancement of the approach described by Moore *et al.* (1976) and refined by Ali (1973) and Rhue (1976). This enhancement is the addition of a stain which permits a rapid visual scoring of test results, in a way similar to the haematoxylin test, and avoids measuring root length.

The method is identical to the haematoxylin test for the first three days. The aluminium exposure is for 48 hours rather than 16 hours as in the haematoxylin test and the aim is to cause irreversible damage (i.e. death) of the growing points of the roots in sensitive cultivars as outlined by Moore *et al.* (1976). At the completion of the aluminium exposure, the roots are stained, simply to mark which ones were exposed to the aluminium. The plants remain on the rafts during staining as described by Polle *et al.* (1978) for the haematoxylin staining. The rafts are then floated on a nil aluminium, recovery solution for three days. Fig. 4 shows the results of a test run with a sensitive and a tolerant cultivar of wheat. Death of the growing point of the root has occurred with the sensitive but not with the tolerant cultivar and this is made obvious by the unstained root growth. We used a peroxidase stain but we have not fully evaluated the effects of the stain on root growth. However, neutral red may be suitable (Schumacher *et al.*, 1983).

Apart from rapid visual scoring, the test shares a number of advantages with the haematoxylin test. These are that seed and not seedlings are handled during the test, the total duration of the test is short (seven days cf. four days in the haematoxylin test) and the duration of the aluminium exposure is short. This means that first, phosphorus need not

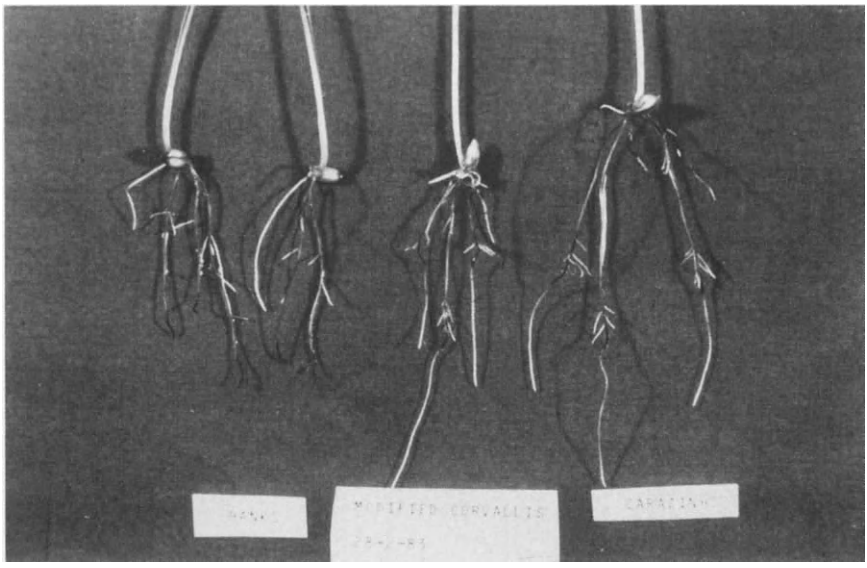


Fig. 4. Seven-day-old seedlings of the wheat cultivars 'Banks' (Australian, aluminium-sensitive) and 'Carazinho' (Brazilian, aluminium-tolerant) after three days growth with no aluminium in solution, two days exposure to aluminium, followed immediately by staining and a three day recovery with no aluminium in solution.
The growth in the recovery solution is unstained and shows that the growing point of the root of the sensitive cultivar was killed but that of the tolerant cultivar continued to grow.

be added, although it could be added to the recovery solution if necessary, and second, the pH and nutrient solution control is only vital for the time of the aluminium exposure. Indeed, the recovery solution need only be controlled broadly and it has been our practice to permit recovery to take place over a weekend without supervision.

The major advantage of our tests over other tests is that it appears to be suitable for a wider range of crops as the death of the growing point of the root under aluminium stress is probably a universal effect on plants. Also death of the growing point is probably not essential and differential root elongation could be the basis of cultivar differentiation. In establishing the test in other species, there would need to be changes in the aluminium levels tested, the nutrient solution at aluminium exposure, the duration of exposure and recovery, and the stain used. We have had success with wheat and barley.

Aniol *et al.* (1980) also used a similar methodology on rye, triticale and wheat. The roots were held in place between chromatography paper

and a lucite plate as described by Konzak *et al.* (1976), and the root tip position was marked on the lucite plate after an aluminium exposure.

Staining may also be useful in replacing the first measurement in tests such as that of Hanson and Kamprath (1979) in which root growth was measured twice in 48 hours of aluminium exposure. Staining at the beginning of the aluminium exposure and measurement from the area of stain to the root tip 48 hours later would give the root growth during the aluminium exposure.

Tests available for assessing manganese tolerance are not as well researched as those for aluminium. As a result they are largely confined to relatively long duration (four to eight weeks) experiments in a manganese-toxic soil or in sand or solution culture. The only alternative method of identifying tolerance seems to be that of Horst (1982; 1983) who described the direct application of manganese to the petioles of intact plants of cowpea and found the symptoms induced to be related to tolerance information obtained from a sand culture experiment.

All the rapid tests described here are non-destructive and use scores of toxicity symptoms, stain patterns or root length measurements or estimates. This permits the plants tested to be grown to maturity. For a breeder these tests mean that plants can be assessed for tolerance and used in a crossing program or grown for seed.

C. Sources of tolerance

1. Within species

The most convenient sources of tolerance to use are those that occur within the same species, provided that an adequate level of tolerance can be achieved. Differences within species for tolerance to the various facets of soil acidity have been reviewed extensively (Wright and Ferrari, 1976; Foy and Fleming, 1978; Foy, 1983a). The identification of the most tolerant lines for use in a breeding program usually involves screening large numbers of collections. Collections expressing tolerance are more likely to be identified from areas with acid soil, like the lateritic soils of Brazil. Takagi (1984) reported that in 686 common wheat cultivars from 15 countries, only four highly tolerant lines were identified and these were from Brazil. Slootmaker and Reid (unpublished data, cited by Reid *et al.*, 1980) tested 1795 barley lines in the USDA world collection and identified 180 lines to use in a composite cross. Barley composite cross XXXIV provides a diverse gene pool made up of segregates from all known lines tolerant of aluminium and/or acid soils (Reid *et al.*, 1980). Howeler (1973) tested approximately 1000 cultivars of rice from various

parts of the world for aluminium tolerance when searching for suitable parental material.

2. Related species

If adequate tolerance is not available within a crop species, it may be possible to introgress the genes for tolerance from related species. Breeding highly acid-tolerant cultivars of the legume *Centrosema pubescens* appeared to be impossible, however selections from crosses between *C. pubescens* and *C. macrocarpum* provided a basis for breeding highly acid-tolerant lines with desirable agronomic characters (Hutton, 1981).

However, the expression of genes from related species is often modified when they are transferred. Differences within the Triticinae have been reported by Slootmaker (1974) and Takagi (1984). The best tolerance to aluminium is present in rye and this tolerance is expressed in triticales. Lopez-Benitez (1977) has investigated the possibility of transferring this tolerance to wheat and found that the rye tolerance was not additive to the tolerance already found in wheat. Modifier genes from the wheat genotype influenced the expression of the full level of tolerance to aluminium contributed by the rye parent in the amphidiploids. Choudry (1980) has studied the addition of a single pair of rye chromosomes to wheat and their effect on wheat tolerance. No transfer of a single chromosome pair markedly improved tolerance in the wheat to which it had been added, suggesting that the rye tolerance is probably multigenic. Aniol and Gustafson (1984) tested rye additions and substitutions in different wheat cultivars and found a reduced expression of the rye tolerance in the wheat background.

The CIMMYT wheat cultivar Alondra (Anon., 1984) or Alondra 'S' (Anon., 1978) has been observed to grow well on the acid soils in Brazil, although it appears to be sensitive to aluminium in laboratory testing, presumably using the haematoxylin stain test. This caused interest as the line carried a rye translocation from the wheat cultivar Weique-Red Mace (Anon., 1978). These reports have attributed the success of Alondra in the field to its resistance to *Septoria* and/or its improved efficiency in phosphorus uptake.

At Wagga Wagga we have tested the tolerance of Alondra (Australian Wheat Collection number 21831) to aluminium and manganese in solution culture and found it to be highly tolerant of both (Figs. 5 and 6) and thus predict that it would perform well on acid soils. The source of the seed was originally Brazil but it arrived in the Australian collection from Corvallis, Oregon (Syme, pers. comm.) and it is believed to be Alondra 4546. There are several possible explanations for the difference

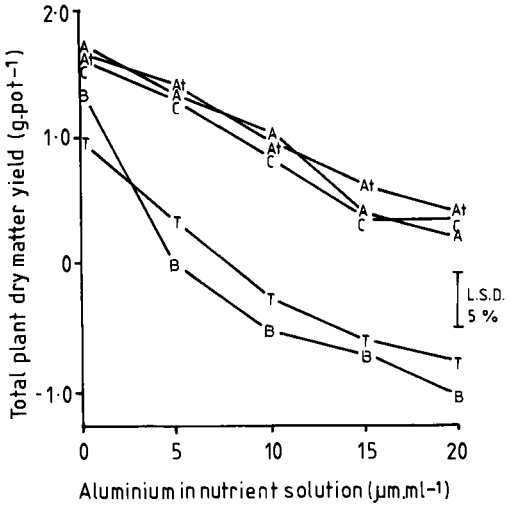


Fig. 5. The effect of aluminium concentrations in solution on the dry matter yield ($\log_e$) of five cultivars of wheat rested at Wagga Wagga, New South Wales. The plants were grown for four weeks in a sub-irrigated gravel bed system similar to that described by Hutton *et al.* (1978). The wheat cultivars are Carazinho (C), Atlas 66 (At), Alondra (A; Aus 21831), Teal (T) and Brevor (B). The first three cultivars are clearly tolerant of aluminium, Teal is intermediate and Brevor is aluminium sensitive.

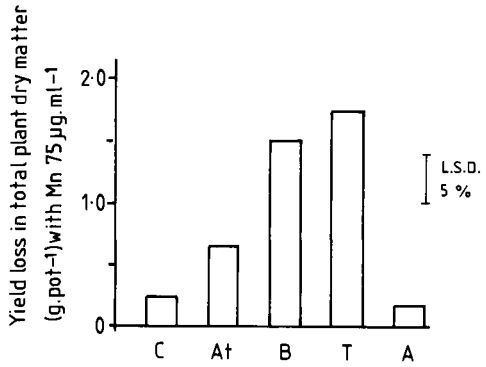


Fig. 6. In the same experiment as described for Figure 5, a treatment with manganese at 75 $\mu g.mL^{-1}$ was tested. The total dry matter yield losses ($\log_e$ yield at Mn_0 — $\log_e$ yield at Mn_{75}) are presented. The wheat cultivars are Carazinho (C), Atlas 66 (At), Alondra (A; Aus 21831), Teal (T) and Brevor (B). Teal was the most manganese-sensitive cultivar (largest yield loss), Brevor was also sensitive, Atlas 66 was intermediate and Carazinho and Alondra were tolerant of the manganese level tested.

between this observation and those of CIMMT. These are that Alondra (Aus 21831) is different to the material tested by CIMMYT, despite the similar name, or that the cultivar has an anomalous reaction with the haematoxylin test.

3. Mutation breeding

Mutation breeding offers the possibility of developing novel properties in existing crop plants. In crops where the desired trait is already available from other sources, mutation breeding offers the prospect of producing a simply modified cultivar (produced maybe by one or two generations of inbreeding) which might then be released very rapidly (Mayo, 1980). However, because of the low frequency of desirable mutants, a very efficient screening system is essential for mutation breeding to be successful.

4. Somaclonal variation

In recent years a new source of variability, somaclonal variation, has become available to breeders. The value of somaclonal variation to plant improvement depends on the ease with which a given plant species can be cultured and plants regenerated from cell lines. Somaclonal variation may find its greatest application for plant improvement in concert with selection for desirable mutations at the cellular level (Nabors, 1976; Scowcroft and Larkin, 1982).

Genotypic differences in aluminium tolerance have been demonstrated in cultures of tomato cells (Meredith, 1978a) and it was possible to select aluminium resistant variants. However, it was not possible to regenerate plants from the cell cultures (Meredith, 1978b). Meredith's experiments show that aluminium tolerance is not exclusively a whole-plant phenomenon even though most of the proposed mechanisms for tolerance operate at the whole-plant level (Section II, A).

5. Recombinant DNA

Recombinant DNA technologies also have the potential for introducing tolerance to acid soils into a cultivar. These techniques require detailed understanding of the genetics and biochemistry of tolerance, as well as a suitable vector for introducing the new DNA sequence into the target species. As yet, nobody has reported the use of this new technology in breeding plants for acid soils.

D. Heritability of tolerance

Breeders will aim, wherever possible, to use major genes in preference to polygenic variation. Selection of traits determined by a few genes of pronounced effect is much more effective in achieving genetic gains than selection for traits determined by many genes with small effects (Mayo, 1980). Rarely is a trait controlled by one class of gene only. More commonly a trait is controlled by a few genes of major effect, a larger number of genes with moderate effects and many genes whose effects are too small to be identified individually.

If selection for a few genes with major effects can give an adequate level of response, then a breeding strategy such as backcrossing can be adopted. This breeding program can be relatively small and the probability of producing the desired cultivar is high. If it is necessary to select for minor genes, large populations are required and the rate of progress and probability of success are lower. When both classes of genes are selected for, it is often advantageous to ensure that the population is homozygous for the major genes before selecting for the minor genes.

1. Aluminium

a Major genes The existence of major genes for tolerance to aluminium has been reported in a number of species. The wheat cultivar, Druchamp, has a major dominant gene compared to the susceptible cultivar, Brevor (Kerridge and Kronstad, 1968). Sensitivity to aluminium in Redcoat and Arthur compared to Seneca and Thorne was conditioned by a single recessive gene (Campbell and Lafever, 1978). Camargo (1981) reported a single dominant gene for tolerance in BH-1146, which was effective at 10 $\mu g.m^{-1}$ of aluminium in solution culture, and two dominant genes in Atlas 66 which were less effective at high levels of aluminium.

There are a number of reports on the location of genes controlling aluminium tolerance in wheat. Chromosome 4D carries a gene controlling aluminium response (Polle *et al.*, 1978). Chinese Spring has genes for aluminium tolerance located on chromosome arms 4Ds and 2Ds (Takagi, 1984). However, Aniol and Gustafson (1984) using Chinese Spring nullisomic-tetrasomic and ditelosomic lines concluded that aluminium tolerance was located on chromosome arms 6A1, 7As, 2D1, 3D1, 4D1, 4B1 and chromosome 7.

Reid (1970) showed that the difference in aluminium tolerance between Dayton and Smooth Awn 86, a winter barley, was controlled by a single dominant gene. Stolen and Anderson (1978) reported that in

barley a single dominant gene located on chromosome 4 controlled tolerance to low soil pH. They suggested that the gene may be synonymous with that reported by Reid (1970) for aluminium tolerance.

In maize a single major gene for aluminium tolerance was reported by Rhue *et al.* (1978) and, to account for the observed range in tolerance among inbred lines, they suggested a multiple allelic series at a single locus. Mortinez-Racines (1977) indicated that tolerance in Monolaya and Bluebonnet 50 rice cultivars, was conditioned by two recessive genes. In grain sorghum, Boye-Goni (1982) concluded that the aluminium tolerant trait was simply inherited. In phalaris, reaction to aluminium can be largely explained by a two-gene model, with tolerance requiring at least one dominant allele at each locus (Culvenor *et al.*, 1986b).

b Quantitative inheritance While the existence of these major genes has been noted, most of the authors also indicated that the major genes account for only part of the observed variation. Campbell and Lafever (1978) found that, in wheat, inheritance of aluminium tolerance was more complex than a single gene with incomplete dominance. To achieve a level of tolerance equivalent to the older Ohio cultivars would require selection for the minor genes affecting aluminium tolerance. Heritability estimates reported for Redcoat/Thorne and Redcoat/Seneca were 0.41 and 0.79. However, these estimates would be affected by the segregation of the major gene for susceptibility. Camargo *et al.* (1980) also examined the quantitative inheritance of aluminium tolerance in wheat and reported that the parent-progeny regression estimate for aluminium tolerance was high ($b = 0.9$). In southern New South Wales, it appears that backcrossing a major gene for aluminium tolerance into a susceptible cultivar may not achieve the desired improvement in tolerance, and selection for minor genes will also be necessary (Fisher and Scott, unpublished data).

Culvenor *et al.* (1986b) obtained heritability estimates between 0.48 and 0.75 for relative root extension after eliminating the sensitive class which lacked one or both of the genes needed for tolerance. However, heritability estimates were low for shoot growth in a field site high in aluminium, possibly due to site variability.

2. Manganese

Tolerance to high levels of exchangeable manganese in lettuce was controlled by from one to four genes in different cultivars (Eenink and Garretsen, 1977). In lucerne, Dessureaux (1959) reported that genes controlling manganese tolerance were additive and the heritability of

tolerance was high. Brown and Devine (1980) concluded that control of tolerance to excess manganese in soybeans was multigenic rather than controlled by a single locus. Reciprocal differences in progeny suggested that cytoplasmic inheritance also influenced manganese tolerance. Heenan *et al.* (1981) also concluded that minor genes were important in the inheritance of manganese tolerance in soybeans, although it was suggested that a single gene may influence tolerance to high levels of manganese in the cross Bragg x Amredo. In wheat, a few genes appear to account for a substantial proportion of the variation in manganese tolerance, and these can be selected successfully in a backcrossing program (Scott and Fisher, unpublished data).

F. Genetic correlations with acid soil tolerance

There is a fear that plants tolerant of acid soils may be essentially low yielding and, in addition, may be poorly adapted to non-acid soils. The notion that cultivars tolerant of acid soils are low yielding occurred because the traditional cultivars grown in acid soil areas were both acid soil tolerant and low yielding when compared with the modern, high yield potential 'green revolution' cultivars. These newer cultivars had not been selected for acid soil tolerance.

In wheat, the tall Brazilian cultivars were the most tolerant of acid soils (Takagi, 1984). In upland rice, the tall traditional cultivars were, in general, rather tolerant while the new dwarf cultivars were more susceptible (Howeler, 1973). As a result it was assumed that these tall, low-yielding characteristics were likely to be linked with aluminium tolerance. This has not proved to be the case in wheat (Anon., 1980a; Camargo *et al.*, 1980). The genetic correlations between aluminium tolerance and plant height or grain yield were not significant.

In Australia some cultivars of wheat, reasonably tolerant of aluminium, have been bred and selected in areas of non-acid soils e.g. Timgalen and Gamenya from northern New South Wales. Should aluminium tolerance be a disadvantage on a non-acid soil, it would be expected that selection pressure would be towards aluminium sensitive cultivars in non-acid areas. The example given suggests that this is not occurring. Similarly with manganese tolerance in wheat, 'Sunstar', a cultivar with considerable manganese tolerance, has been selected in northern New South Wales in the absence of manganese toxicity (authors' unpublished data).

With lucerne, selections made on an acid soil performed better at all pH levels and not just at low pH. These selections were also more responsive to phosphorus application than other germplasm (Bouton and

Sumner, 1983). In soybeans, inefficiency in absorption or utilisation of iron is independent of tolerance to manganese toxicity (Brown and Devine, 1980)

In aluminium-tolerant plants, yield increases have been obtained with the addition of small amounts of aluminium in solution experiments. This has reinforced the claim that tolerant plants may be low yielding in non-acid situations. These increases have been summarised by Foy (1984), but there is no evidence that aluminium is an essential plant nutrient.

In summary, while there is much speculation on adverse correlations with acid soil tolerance, we conclude that there is little evidence in the literature of such problems.

F. Examples of breeding programs

A joint breeding program was commenced by CIMMYT and some Brazilian research institutes in 1973 to transfer tolerance to aluminium into high-yielding semi-dwarf wheats. The tolerance was located primarily in tall, low-yielding, poor agronomic types of wheat. The selection program used a 'shuttle breeding' technique with field tests for tolerance to acid soils in Brazil, laboratory tests for aluminium tolerance in Mexico and selection for disease resistance and other aspects of agronomic performance in Mexico. This program led to Alondra 4546 being released in Parana State of Brazil and many elite lines are now available in the Aluminium Screening Nursery (Anon. 1978, 1980a, 1980b, 1984).

In addition to our program at Wagga Wagga, breeding for tolerance to acid soils in wheat is also being undertaken in Western Australia (Barclay, 1985). These two Australian breeding programs aim at the release of commercial cultivars.

Germplasm tolerant of acid soils has been registered for a number of crops, for example barley (Composite Cross XXXIV; Reid *et al.*, 1980), crownvetch (*Coronilla varia* L.; Virginia Synthetic; Miller, 1980) and sorghum (GPIR; Duncan, 1981).

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